Rainbow Smelt – Larval Lake Herring Interactions: Competitors or Casual Acquaintances?

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By

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Abstract. We examined the hypothesis that competition for food between rainbow smelt (*Osmerus mordax*) and larval lake herring (*Coregonus artedi*) was a cause for the declines of lake herring stocks in Lake Superior. We studied the diet of larval lake herring and of larval, juvenile, and adult rainbow smelt during 1974 in Black Bay, Ontario, where both species were abundant, and in the Apostle Islands Region, Wisconsin, where rainbow smelt was abundant but lake herring was scarce. No evidence of competition for food was found between larval lake herring and rainbow smelt. Spawning and hatching times of the two species were separate enough that most larvae of the two species did not occupy the study areas simultaneously. Juvenile and adult rainbow smelt were found with lake herring larvae, but their diets differed. Therefore, we concluded that rainbow smelt did not compete with lake herring larvae for food and that competition for food between rainbow smelt and lake herring larvae was not the factor that caused lake herring population declines in Lake Superior.

Key words: Lake herring, *Coregonus artedi*, rainbow smelt, *Osmerus mordax*, competition, Lake Superior.

Historically, more biomass of lake herring (*Coregonus artedi*) was harvested commercially from Lake Superior than of all other fish species combined (Baldwin et al. 1979), so this species probably also constituted more biomass than all other sport or food fishes in the lake. The rainbow smelt (*Osmerus mordax*) is not native to Lake Superior but invaded the lake around 1930 (Lawrie 1978), although the species was not abundant enough to support a commercial fishery until 1952 (Baldwin et al. 1979). Competition for food between rainbow smelt and lake herring has been implicated as the probable cause of lake herring declines in Lake Superior during 1949–66 (Anderson and Smith 1971), and collapses of lake herring stocks in the other Great Lakes followed increases in rainbow smelt abundance (Christie 1974). The circumstantial evidence that resulted after the invasion or introduction of rainbow smelt in other waters has led researchers to conclude that competition for food could affect the recruitment of lake herring. Because newly hatched larvae eat specific foods (Siefert 1972), they are vulnerable to starvation if competition for limited food resources is severe. Competition could be important in determining year-class strengths and could eventually result in severe reduction or elimination of a species.

Gordon (1961) concluded that rainbow smelt in Saginaw Bay, Lake Huron, competed for food with young fish of all species and the adults of some, although he did not study the diet of sympatric lake herring. Creaser (1927, 1929) also suggested that the abundance and diet of rainbow smelt might make them important competitors with lake herring. Anderson and Smith (1971) stated that food similarities between early life stages of lake herring, rainbow smelt, and bloater (*C. hoyi*) indicated that competition for food had a strong influence on the decline of lake herring stocks. Anderson and Smith (1971) found significant negative correlations and linear trends between Lake Superior lake herring and rainbow smelt abundance and between lake herring and bloater abundance. Anderson and Smith (1971) stated that the rainbow smelt was probably a more influential competitor with lake herring than was the bloater. Bloater and lake herring co-evolved and had apparently existed together for centuries. In the 1970's and 1980's bloater populations in Lake Superior declined greatly without concomitant increases of lake herring stocks. We doubt that the bloater was a major cause of the decline in lake herring stocks. No studies have been published that have demonstrated competition for food between larval lake herring and rainbow smelt.

To evaluate Anderson and Smith's (1971) conclusion that competition for food between rainbow smelt and lake herring larvae was substantial, we examined whether competition for food was occurring between rainbow smelt and larval lake herring that could affect the survival of the larvae and the year-class strength of lake herring. The objective of our study was to document the diet of larval lake herring and of larval, juvenile, and adult rainbow smelt to determine the level of competition for food between the species. The study was conducted in the Apostle Islands region of Wisconsin and in Black Bay, Ontario, during spring 1974. We selected Black Bay as a study area because it was the only portion of Lake Superior that still supported a large fishery for lake herring (and presumably a large spawning population) in 1974 (Selgeby et al. 1978). We selected the Apostle Islands area because it had formerly supported a large population of lake herring that had declined about a decade after the increase in the commercial fishery for rainbow smelt (Baldwin et al. 1979) and because this was one of the areas studied by Anderson and Smith (1971), who concluded that competition with rainbow smelt probably caused the decline in lake herring stocks. Lake herring spawning stocks in the Apostle Islands region were small in 1974 as the result of a sharp decline during the 1950's (Baldwin et al. 1979; Selgeby 1982). Rainbow smelt stocks were relatively large in 1974, as indicated by the increasing commercial harvest in Wisconsin waters—from 454 kg in 1949 to 214,095 kg in 1974 (Baldwin et al. 1979).

Methods

Sampling was done at dusk and dawn at two stations in Black Bay and at six stations in the Apostle Islands region (Fig. 1). Zooplankton sampling at each station in Black Bay consisted of a surface-to-bottom-to-surface (double oblique) tow with a Clarke-Bumpus sampler (number 10 mesh net). One 10-min tow with a 1-m^2 net about 0.5 m below the surface was taken to collect lake herring and rainbow smelt larvae, and three or four 10-min tows were made with a 4.8-m (footrope) otter trawl on the bottom to collect yearling and older rainbow smelt. Sampling at each station in the Apostle Islands region consisted of one double-oblique tow with a Clarke-Bumpus sampler and horizontal tows near the surface and at 10-m depth intervals
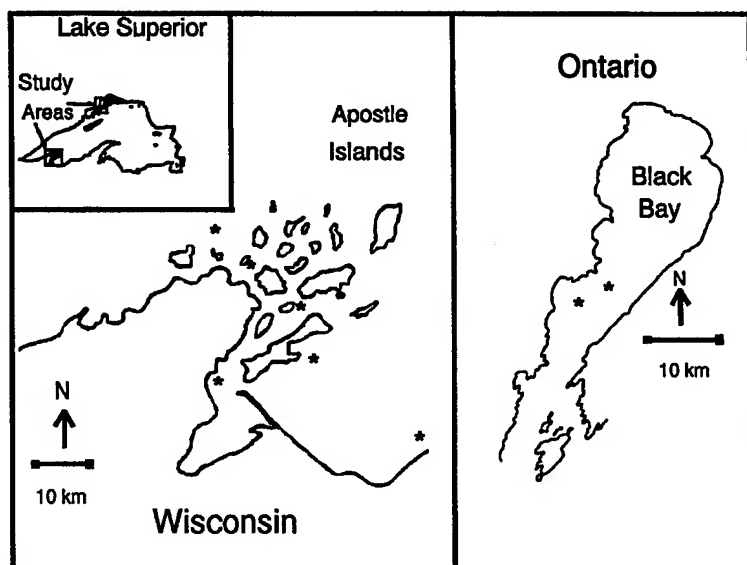
Fig. 1. Sampling sites (*) for lake herring larvae and rainbow smelt in Black Bay and the Apostle Islands region, Lake Superior.

to the bottom with a 1-m² net and 4.8-m trawl. All samples of lake herring larvae and most catches of rainbow smelt were preserved in formalin, although only subsamples of rainbow smelt were used when catches were large.

Sampling began in both areas within a few days after the ice melted. Sampling was done on 6–8 May, 13–15 May, 28–30 May, 11–13 June, and 1–3 July in the Apostle Islands region and on 25–26 May, 30 May, 9 June, 12 June, 19 June, 25 June, 6 July, and 11 July in Black Bay.

Food of lake herring larvae was determined as follows: Larvae were measured microscopically to the nearest 1.0 mm and were separated into 1-mm length classes. Fifty larvae in each length class, or the total in that class if less than 50 were collected, were selected from each sampling period. Stomachs were removed, opened, and examined for food. Presence or absence of food was noted for individual larvae, but food items were combined to form composites by 1-mm length class and by sampling period. Samples of food items, and of zooplankton collected with the Clarke-Bumpus sampler, were processed by identification to species (except that copepod nauplii and copepodids were grouped) and by counting totals or subsamples. Densities (number per cubic meter) of zooplankton and of rainbow smelt and lake herring larvae were calculated based on the volume of water filtered by the appropriate collection device.

Rainbow smelt stomachs were processed after measuring (total length in millimeters) and weighing (grams) each fish. The stomach was then removed and weighed, the contents extracted, and the empty stomach weighed. Weight of the contents was calculated by subtracting the weight of the empty stomach from that of the stomach with food. The contents of each stomach were examined microscopically. Average ash-free dry weights of individual organisms in the food were determined from intact organisms after drying at 100° C for 24 h and ashing at 550° C for 1 h.

Results

Abundance of Lake Herring Larvae and Rainbow Smelt

Lake herring larvae were collected during 6 May–7 July in the Apostle Islands region (Fig. 2) but only during 25–30 May in Black Bay. The sampling period with the greatest maximum geometric mean density in the Apostle Islands region was 28–30 May. The geometric mean density (±SE) of larval lake herring was high in Black Bay during the 25–30 May sampling period (1,260 ± 240/1,000 m³) compared with the highest mean for the Apostle Islands region (10 ± 1/1000 m³).

Rainbow smelt larvae were collected in the Apostle Islands region in small numbers on 11–13 June and in larger numbers on 1–3 July. In Black Bay, rainbow smelt larvae were first taken on 9 June, and they were abundant on 6 July. Thus, in the Apostle Islands region the greatest density of rainbow smelt larvae was found 2 weeks after the peak in larval lake herring abundance. In
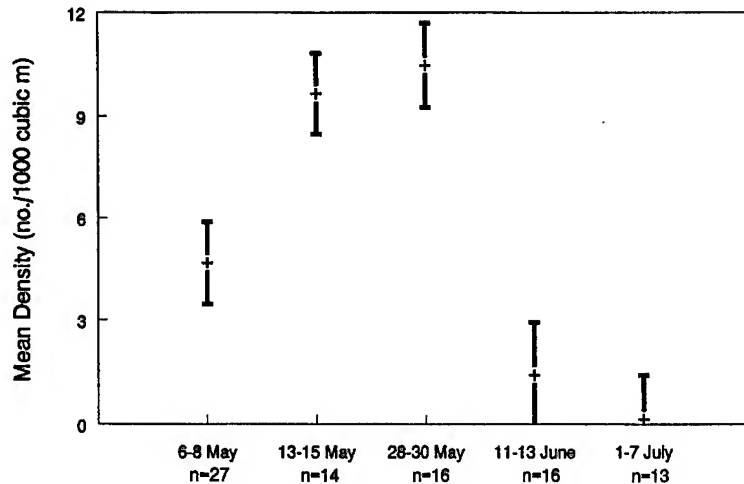
Fig. 2. Geometric mean (±SE) densities at six index stations in the Apostle Islands region, 1974. The number of 1-m^2 net hauls (10-min tows) is shown for each sampling period.

Black Bay, larval rainbow smelt were not found simultaneously with larval lake herring.

Juvenile (age 1) and adult (age 2 and older) rainbow smelt were present in both areas throughout the sampling period. During rainbow smelt spawning, which coincided with the period lake herring larvae were collected, rainbow smelt catch-per-unit-of-effort (CPUE) was three times as high in Black Bay as in the Apostle Islands region. After spawning, substantial rainbow smelt mortalities occurred in Black Bay, and some rainbow smelt may have left the bay because CPUE declined to about the same level as in the Apostle Islands region. Average CPUE, over the entire study period, was about 40% higher in Black Bay than in the Apostle Islands region.

Abundance and Composition of Crustacean Zooplankton

The crustacean zooplankton of Black Bay was more abundant and diverse than that of the Apostle Islands region (Table 1). Total crustacean density averaged 9,080/m^3 in Black Bay and 2,906/m^3 in the Apostle Islands region. Ten species of copepods and seven species of cladocerans were found in Black Bay, whereas only six species of copepods and three species of cladocerans were found in the Apostle Islands region. No crustacean species were found in the Apostle Islands region that were not also found in Black Bay. In both areas, changes in zooplankton populations during the sampling period were related mainly to the life histories and seasonal cycles of the component species. Abundance of immature copepods in Black Bay declined during the first few days that lake herring larvae

were present, but following that decline, and during the period larvae were still very abundant, immature copepods increased about 10-fold in abundance.

Food and Feeding of Lake Herring Larvae

Food and feeding of lake herring larvae were similar in Black Bay and the Apostle Islands region (Table 2). We interpreted our data on the proportion of larvae with food in their stomachs as an index of feeding behavior (Fig. 3). Some larvae began feeding shortly after hatching, probably within 1 day after hatching, as previously described by John and Hasler (1956). The proportion of larvae with food in their stomachs increased rapidly from 19% for 9-mm fish to 97% for 14-mm fish, after which length the proportion with food stabilized. This plateau either indicated that some larvae never began feeding or, more likely, that the interval for gastric evacuation was less than the interval between feeding periods. These data demonstrated that lake herring larvae did not pass through a critical feeding period of a few hours or days in the two study areas during 1974 because endogenous feeding overlapped with the initiation of exogenous feeding. Even at lengths of 17 mm, a small yolk supply remained, and all lake herring larvae had begun feeding before reaching that size. Hogman (1971) found that larval lake whitefish (*C. clupeaformis*) in Lake Michigan also began feeding before the yolk supply was fully utilized.

The diet of lake herring larvae was dominated by immature copepods. Copepod nauplii, immature

Table 1. Average density of crustacean zooplankton in Black Bay and the Apostle Islands region of Lake Superior during May–July 1974.

Taxon	Black Bay 25 May–11 July (no./m^3)	Apostle Islands region 6 May–3 July (no./m^3)
Sample number	18	30
Copepoda		
Nauplii	3,387.1	1,820.6
Immature Calanoida[a]	1,724.6	347.4
Adult Calanoida		
Diaptomus sicilis	113.1	420.5
Diaptomus ashlandi	26.9	56.6
Diaptomus minutus	185.7	0.0
Diaptomus oregonensis	228.9	0.0
Limnocalanus macrurus[b]	34.7	82.5
Senecella calanoides[b]	1.7	1.4
Epischura lacustris[b]	43.1	0.6
Immature Cyclopoida	1,629.8	98.0
Adult Cyclopoida		
Cyclops bicuspidatus thomasi	986.5	72.2
Cyclops vernalis	9.4	0.0
Mesocyclops edax	3.2	0.0
Cladocera		
Daphnia retrocurva	254.3	0.6
Daphnia galeata mendotae	96.2	1.4
Bosmina longirostris	332.6	4.2
Leptodora kindtii	9.4	0.0
Diaphanosoma leuchtenbergianum	10.8	0.0
Chydorus gibbus	0.8	0.0
Sida crystalina	1.4	0.0
Total	9,080.2	2,906.0

[a] Does not include immature *Limnocalanus macrurus*, *Senecella calanoides*, or *Epischura lacustris*.
[b] Includes all copepodid stages.

Table 2. Food of larval lake herring during 6 May–7 July 1974 in the Apostle Islands region and Black Bay, Lake Superior.

Taxon	Apostle Islands[a] Total no. of food items	Percent of total food items	Black Bay[b] Total no. of food items	Percent of total food items	Apostle Islands and Black Bay Total no. of food items	Percent of total food items
Copepoda nauplii	1,501	63.0	5	3.2	1,506	59.3
Diaptomus sp. - immature	401	16.8	38	24.1	439	17.3
Unidentified Cyclopoida Copepoda - immature	221	9.3	52	32.9	273	10.8
Diaptomus ashlandi	227	9.5			227	8.9
Notholca sp.	8	0.3	52	32.9	60	2.4
Limnocalanus macrurus	3	0.1	9	5.7	12	0.5
Daphnia sp.	4	0.2			4	0.2
Diaptomus sicilis	4	0.2			4	0.2
Cyclops bicuspidatus thomasi	2	0.1	2	1.3	4	0.2
Acroperus harpae	3	0.1			3	0.1
Unidentified Rotifera	3	0.1			3	0.1
Polyphemus pediculus	2	0.1			2	0.1
Bosmina longirostris	1	<0.1			1	<0.1
Epischura lacustris	1	<0.1			1	<0.1
Total	2,381	99.8	158	100.1	2,539	100.1

[a] 1,000 stomachs examined from fish collected during May 6–July 7, 1974; 728 of the stomachs contained food.
[b] 625 stomachs examined from fish collected during May 23–30, 1974; 143 of the stomachs contained food.
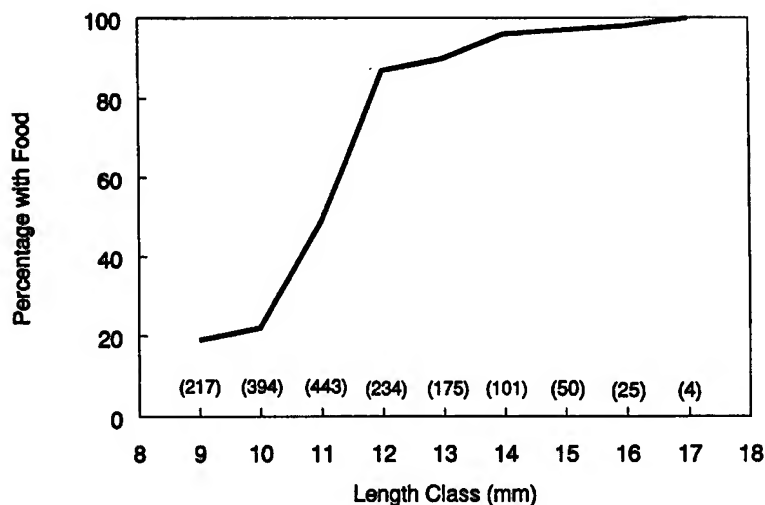
Fig. 3. Percentage of lake herring larvae with food, by 1-mm length classes, from combined samples collected in Black Bay and the Apostle Islands region, May 1974 (number examined in parentheses).

Diaptomus sp., and immature cyclopoid copepods composed 89% of the Apostle Islands lake herring diet during 6 May–7 July 1974, but these same taxa composed only 60% of the food items of Black Bay lake herring larvae collected during 23–30 May 1974. However, the rotifer *Notholca* sp. composed an additional 33% of the food items for Black Bay larvae. Lake herring larvae 9–13 mm long ate more copepod nauplii than copepod copepodids (Fig. 4). The copepodids (about equally divided between young *Cyclops bicuspidatus thomasi* and young (*D. sicilis*) were, however, much larger than the nauplii and formed the bulk of the food. Lake herring larvae of these lengths also ate a few rotifers. Consumption of nauplii declined among lake herring larvae longer than 13 mm, while consumption of rotifers ceased and consumption of copepodids

increased (a few immature *Limnocalanus macrurus* were eaten by larvae longer than 13 mm). Besides copepods, lake herring larvae ≥13 mm ate a few small cladocerans such as immature *Polyphemus pediculus*, *Daphnia galeata mendotae*, and *Bosmina longirostris*.

Food of Rainbow Smelt

No larval rainbow smelt collected during May in the Apostle Islands region, or in early June in the Apostle Islands region or Black Bay, contained food. Larval rainbow smelt collected in late June and July contained mainly copepod nauplii.

Food of juvenile rainbow smelt was similar across size classes, as was that of adult rainbow smelt, but food of these two groups differed. Food
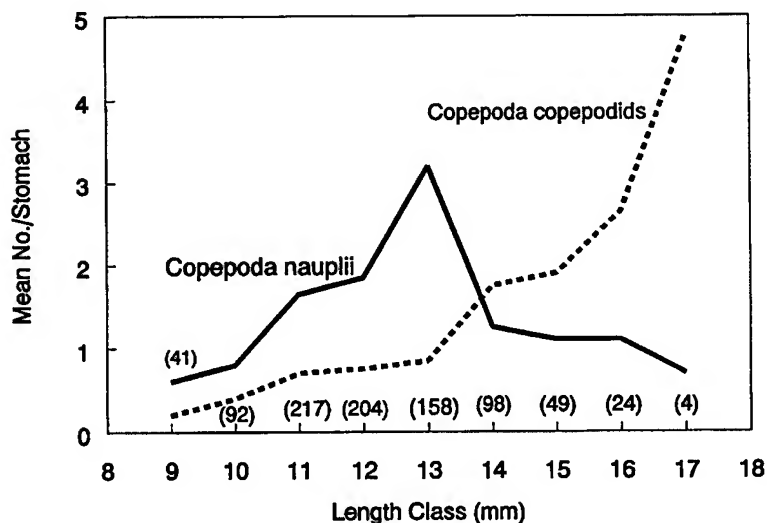

Fig. 4. Food of lake herring larvae, by 1-mm length classes, May 1974.

items were pooled for 10-mm size classes within the two age groups.

We examined 1,711 rainbow smelt stomachs from the Apostle Islands region, of which 1,146 (67.0%) contained food that constituted an average of 0.51% of body weight. Juvenile rainbow smelt ate mainly adult *D. sicilis* (81.6% by number and 74.7% by weight; Table 3). Juvenile rainbow smelt contained food that constituted an average of 0.56% of body weight. Adult rainbow smelt contained food equal to 0.35% of body weight. Adult rainbow smelt ate fewer zooplankton food items than did juvenile rainbow smelt. *Diaptomus sicilis* was the most abundant organism eaten by adult rainbow smelt (54.3% by number), but the burrowing amphipod *Pontoporeia affinis* composed 82.1% of the biomass eaten.

During the period that lake herring larvae were present in Black Bay, we examined 1,195 rainbow smelt stomachs, of which 685 (57.3%) contained food that constituted an average of 0.79% of body weight. Juvenile rainbow smelt contained food that constituted an average of 0.69% of body weight. Juvenile rainbow smelt ate mainly the copepod *D. sicilis* (91.3% by number), but lake herring larvae composed most (66.2%) of the food biomass (Table 4). Adult rainbow smelt contained food equal to 1.54% of average body weight. Adult rainbow smelt ate mainly lake herring larvae, by number (69.4%) and weight (94.4%). Of the 685 adult rainbow smelt with food in their stomachs, 204 (29.8%) contained lake herring larvae. Twenty-three percent of the juvenile rainbow smelt (136 of 604) and 84.0% (68 of 81) of the adult rainbow smelt contained lake herring larvae. From these same data,

Selgeby et al. (1978) examined the hypothesis that predation by rainbow smelt on lake herring larvae during 1974 was the major factor that affected lake herring stocks in either area.

Discussion

Nearly all of the lake herring larvae began feeding before the yolk sac was fully absorbed. Rainbow smelt spawned at about the same time that lake herring began hatching, and rainbow smelt larvae were first collected after the peak in the abundance of lake herring was measured. The temporal separation of the larvae of the two species was complete in Black Bay and nearly complete in the Apostle Islands region. Thus, competition for food between the larvae of these fishes was almost nonexistent. Although juvenile and adult rainbow smelt occupied the same areas as lake herring larvae, they ate different invertebrate species or life stages than did lake herring larvae. The food of larval lake herring in both study areas was composed mainly of copepod nauplii and larger immature copepods. These food items were not found at all in the stomachs of juvenile and adult rainbow smelt in either study area. Because the food items that dominated the diet of larval lake herring were abundant in both study areas and did not become scarce during the period of larval feeding, and because there was nearly no overlap in diet between the two species, we conclude that competition between larval lake herring and rainbow smelt did not affect year-class strengths of lake herring in the two study areas during 1974.

Table 3. Food of rainbow smelt in the Apostle Islands region of Lake Superior, 6 May–3 July 1974.

	Diaptomus sicilis	Diaptomus ashlandi	Cyclops b. thomasi	Limnocalanus macrurus	Senecella calanoides	Mysis relicta	Pontoporeia affinis	Chironomid pupae
Juvenile smelt[a]								
Percent by number	81.6	13.3	0.9	0.7	0.9	0.0	1.0	0.8
Percent by weight	74.7	2.6	0.1	0.7	2.6	0.0	14.2	5.2
Adult smelt[b]								
Percent by number	54.3	6.2	0.0	10.0	3.5	0.3	23.5	2.2
Percent by weight	2.4	0.1	0.0	2.5	2.5	6.8	82.1	3.6

[a] 1,301 stomachs examined; 844 of the stomachs contained food.
[b] 410 stomachs examined; 302 of the stomachs contained food.

Table 4. Food of rainbow smelt in Black Bay, Lake Superior, 25–30 June 1974.

	Lake herring larvae	Diaptomus sicilis	Diaptomus ashlandi	Cyclops b. thomasi	Limno-calanus macrurus	Mysis relicta	Ponto-poreia affinis	Chironomid pupae	Ephemer-optera nymphs
Juvenile smelt[a]									
Percent by no.	3.1	91.3	0.6	1.0	3.4	0.0	0.4	0.1	0.1
Percent by weight	66.2	26.5	0.1	0.1	2.6	0.0	3.9	0.2	0.5
Adult smelt[b]									
Percent by no.	69.4	21.0	0.2	1.2	2.8	0.2	4.0	0.3	0.9
Percent by weight	94.4	0.2	<0.1	<0.1	0.2	0.7	2.8	0.1	1.6

[a] 1,058 stomachs examined; 604 of the stomachs contained food.
[b] 137 stomachs examined; 81 of the stomachs contained food.

In this analysis, we found that larval lake herring and rainbow smelt are almost completely separated temporally, and lake herring larvae consumed organisms that were abundant and were smaller than those fed upon by juvenile and adult rainbow smelt. Therefore, if competition exists for limited food resources between age-0 lake herring and rainbow smelt, that competition must occur after the larval stage of lake herring. Crowder (1980) speculated that rainbow smelt interacted strongly with lake herring in Lake Michigan, and he felt that predation by rainbow smelt on young lake herring may have been a more important mechanism than competition. If a negative ecological relationship indeed exists between lake herring and rainbow smelt, the cause of the relationship has been difficult to measure, cannot be predicted, or may be variable among waters (Evans and Loftus 1987). Therefore, further research is needed to determine whether the negative population trends between the two species in Lake Superior are the result of biotic or abiotic ecological relationships. We recommend that a study be initiated that will describe the level of competition for food between age-0 lake herring (postlarval stage) and rainbow smelt. The proposed study would further the knowledge of the ecological interactions between these important Lake Superior fishes.

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National Biological Survey

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